Available online at www.sciencedirect.com
ScienceDirect
South African Journal of Botany 74 (2008) 432–444
SOUTH AFRICAN JOURNAL OF BOTANY
www.elsevier.com/locate/sajb

Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa

S. Vosse [a], K.J. Esler [a,*], D.M. Richardson [b], P.M. Holmes [c]

[a] *Centre for Invasion Biology, Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*
[b] *Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*
[c] *City of Cape Town, Environmental Resource Management Department, Private Bag X5, Plumstead 7801, South Africa*

Received 15 August 2007; accepted 22 January 2008

Abstract

Riparian zones are complex disturbance-mediated systems that are highly susceptible to invasion by alien plants. They are prioritized in most alien-plant management initiatives in South Africa. The current practice for the restoration of cleared riparian areas relies largely on the unaided recovery of native species from residual individuals and regeneration from soil-stored seed banks. Little is known about the factors that determine the effectiveness of this approach. We need to know how seed banks of native species in riparian ecosystems are affected by invasion, and the potential for cleared riparian areas to recover unaided after clearing operations. Study sites were selected on four river systems in the Western Cape: the Berg, Eerste, Molenaars and Wit Rivers. Plots were selected in both invaded (>75% Invasive Alien Plant (IAP) canopy cover) and un-invaded (also termed reference, with <25% IAP canopy cover) sections of the rivers. Replicate plots were established at two elevations (mountain stream and foothill) and in three moisture regimes (dry, wet and transitional bank zones). Soil samples were taken, surveys were done of the aboveground vegetation, and comparisons were made between invaded and non-invaded sites. Seed bank communities were clearly defined by the state of the river (reference or invaded) and moisture regimes (wet and dry bank zones). Comparisons at a landscape scale showed no clear pattern, as the composition of both aboveground and seed bank species assemblages were strongly influenced by site history, especially the extent of invasion and fire frequency. Even after heavy and extensive invasion, riparian seed banks have the potential to initiate the restoration process. However, not all riparian species are represented in the seed bank. Based on these results, restoration recommendations are outlined for alien-invaded riparian zones.

Keywords: Biological invasions; Community recovery; Invasive alien plants; Restoration ecology; Soil-stored seeds; Species assemblages

1. Introduction

Riparian areas worldwide are very susceptible to invasion by alien plant species. This is because of the exposure of riparian vegetation to frequent natural and human-induced disturbances, the dynamic nutrient levels and hydrology, water-aided dispersal of propagules, and the role of stream banks as a reservoir for propagules of both indigenous and exotic species (Rowntree, 1991; Planty-Tabacchi et al., 1996; Galatowitsch and Richardson, 2005; Richardson et al., 2007). Woody invasive alien plants (IAPs) remove large quantities of water daily, changing water table levels (Rowntree, 1991). Invasive species also disrupt vegetation dynamics by altering colonisation ability, thereby affecting vegetation structure and indigenous plant establishment (Cohn, 2001; Muotka and Laasonen, 2002; Ladd et al., 2005). To curb such impacts, the South African government supports various alien-plant clearing initiatives, most of which give priority to river corridors to reduce the spread of propagules along rivers and into adjoining terrestrial areas (Richardson et al., 1997). The largest initiative is the Working for Water (WfW) programme which was launched in 1995 with the aims of improving and increasing both the quality and quantity of water, conserving biodiversity, and providing employment (Van Wilgen et al.,

* Corresponding author.
E-mail address: kje@sun.ac.za (K.J. Esler).

0254-6299/$ - see front matter
doi:10.1016/j.sajb.2008.01.170

1998). This programme aims for full recovery of riparian vegetation after removal of the invasive species, but a limited budget precludes active restoration at a large scale (Holmes, 1998, 2001). Inadequate recovery of riparian vegetation can result in soil erosion, loss of soil-stored propagules of native species, poor water quality, and a high risk of re-invasion by alien plant species (Holmes, 2001).

In their study of riparian scrub recovery after alien-plant clearing in the Fynbos Biome, Galatowitsch and Richardson (2005) highlighted the need for research into the recruitment dynamics of disturbed riparian zones. It is important to ascertain whether the main supply of new propagules for recolonisation comes from external sources, via water, wind or animal dispersal, or from *in situ* seed banks stored in the soil. The seed bank is defined as 'a reserve of viable seeds, fruits, propagules and other reproductive plant structures in the soil' (Goodson et al., 2001). Seed bank data can yield information on three features of the potential new vegetation: (1) the species composition, (2) the relative abundance of species, and (3) the distribution of each species (Welling et al., 1988). Additionally, analyses of the compositional data of both the seed bank and aboveground vegetation can reveal which desirable species are lacking in the seed bank and may need to be re-introduced by other means (e.g. replanting). Soil seed banks contribute significantly to the regeneration of plant cover following a disturbance in many vegetation types (Musil and De Witt, 1990; Holmes and Marais, 2000) but little research has focused on riparian zones. Restoration of a degraded landscape usually aims to return the area to some pre-disturbance condition where ecosystem functioning is sustainable in the long term (Rutherford et al., 2000; Richter and Stromberg, 2005). A thorough understanding of the role of seed banks, especially of the most influential species (in this paper assumed to be those that are most common and frequently occurring), is important for designing effective restoration projects.

Much work has been done in terrestrial (Thompson, 1992, 1993; Warr et al., 1993; Goodson et al., 2001; Holmes, 2002) and wetland (Van der Valk, 1981; Welling et al., 1988; Leck, 1989) systems on the dynamics of seed banks. Surprisingly little information is, however, available for riparian seed banks. Many processes are implicated in burying seeds in the soils of riparian ecosystems. Flood water disperses propagules and buries them under sediment (Richter and Stromberg, 2005). Mechanical translocation of soil during damming or canalization may also disperse propagules. Disturbance, and the resulting removal of indigenous vegetation, allows non-native species to become established in riparian systems (Bunn et al., 1998). Bare patches of soil are typically colonized by ruderals and longer-lived competitors (like many riparian tree invaders e.g. *Acacia mearnsii* in South Africa) may replace the ruderals. When open patches reoccur, they may be colonized by residual species that have persisted in the seed bank, or by immigrants dispersed from nearby vegetation patches or off-site seed banks. This process makes riparian zones diverse but also makes them vulnerable to invasion by alien invasive trees and shrubs.

Most restoration projects in invaded systems begin with the removal of alien vegetation, and this is often seen as the final goal. However, in some cases, additional attention may be required to set the system on a trajectory towards recovery of key indigenous species and aspects of ecosystem functioning (Holmes and Richardson, 1999; Galatowitsch and Richardson, 2005; Harms and Hiebert, 2006). A recent North American study on the invasive species Tamarisk (*Tamarix* spp.) found that the removal of aliens alone was inadequate to promote the re-establishment of a healthy riparian community (Harms and Hiebert, 2006). Propagule supply is thought to play a significant role in both alien plant invasion and habitat recovery rate. Renöfält et al. (2005) found that the delivery of propagules by flood events increases plant species richness in un-invaded rivers. However, if the upper catchment is degraded and the seed source depleted (through invasion or deforestation), the down-stream areas are less likely to have successful post-disturbance recovery.

This study investigates the potential of native seed banks in riparian zones of the Western Cape, South Africa, to drive unaided recovery of natural vegetation following mechanical clearing of invasive alien trees and shrubs. By describing seed banks we investigated the following key questions:

- To what extent do riparian seed banks have the potential to regenerate vegetation that is compositionally similar to undisturbed riparian vegetation?
- What happens to the species composition of the riparian seed bank after invasion and is it adequate to initiate ecosystem recovery?
- What are the implications for restoration of riparian vegetation in the Western Cape?

2. Materials and methods

2.1. Data collection

Four river systems within the southwestern part of the Western Cape (Berg, Eerste, Molenaars and Wit Rivers) were chosen for their variety of reach types, history of alien plant invasion, and for their close proximity to the research facilities. Details of the riparian vegetation of three of these rivers (all except the Berg) are provided by Prins et al. (2004). The sampling method combined subjective selection of plots within homogeneous plant assemblages and objective, random placement of sampling quadrats within these plots. Fieldwork at all sites was done during late summer (March–April 2005 and 2006). Plots were selected in both relatively undisturbed areas (also termed reference with <25% alien plant canopy cover) and heavily invaded (considered "closed" alien stands with >75% alien canopy cover) riparian sections of the rivers.

The major zones of the riparian system were sampled on a lateral scale as the aquatic zone, the wet bank zone and the dry bank zone; and on a longitudinal scale as mountain stream and foothill zones (Davies and Day, 1998; Boucher and Tlale, 1999). The aquatic zone was subdivided into a zone that dries up during the dry season and the zone that is always wet. The wet bank zone consists of a sedge zone and a shrub zone, flooded respectively by the low flow and high flow during the wet season. The dry bank is divided into a lower dynamic zone which forms the transition between wet and dry bank zones (referred to in this paper as the transitional zone), the tree/shrub zone where moisture is available only to plant species with a deeper root system, and a lower back dynamic zone where the influence of flooding is experienced only during extreme events and therefore terrestrial vegetation is dominant (Davies and Day, 1998; Boucher and Tlale, in press). Mountain stream zones occur where erosion exceeds sediment accumulation; foothill zones where erosion and accumulation are more or less in balance. Lowland river zones, where accumulation exceeds erosion, were not sampled in this study (Davies and Day, 1998).

At each river reach a plot was established in the riparian vegetation, where the influence of riparian vegetation was evident. Each plot measured twenty metres in length (parallel to the river) and five metres in width (perpendicular to the river crossing both the wet bank and dry bank zones). Where the wet bank zone was distinctive, one 20 m-long transect was placed through the wet bank vegetation and a second transect through the dry bank vegetation. Along each lateral zone transect, ten quadrats (1 m × 1 m) were placed using random numbers to determine their location.

Ecological information was recorded for each quadrat, including species presence and percentage canopy cover, % rock cover and % bare ground, together with an estimate of total canopy cover for the quadrat. Herbarium specimens were collected of seedlings or species that could not be identified on site. Nomenclature in this paper follows Germishuizen et al. (2006), and full details of author's names are provided in Appendix A (available online). Various geomorphological features of the river and the sampling area were noted, including morphological unit (pool, rapid, riffle etc) geology, altitude, aspect, slope and GPS location.

A hand-held soil corer (measuring 5 cm diameter and 10 cm depth) was used to extract the soil samples. Each soil sample comprised 5 cores collected from within the 1 m^2 quadrat then bulked together. Sampling was done across the whole quadrat to encompass spatial variability in the seed bank. This method was then repeated in the dry bank zone, where it was present. Within many mountain stream sections of the rivers, only a narrow riparian vegetation strip was present for sampling, called the transitional bank zone. As a result, plots that incorporated both wet and dry bank zones had 20 samples, while plots that only had a transitional bank zone present had 10 samples. Replicate sites were then sampled along each particular river reach (where possible three mountain stream and three foothill plots per river system) to allow for variability. Within some rivers, only two replicate plots were established as a result of poor site quality, especially within reference foothill sites and invaded mountain stream sites. In total, 22 plots (290 samples) were sampled within the reference plots and 23 plots (310 samples) within the invaded plots, giving a total of 600 samples once combined. All analyses were done at plot level to avoid pseudoreplication.

Soil samples were transported to an open-sided plastic tunnel at the Welgevallen Experimental Farm at Stellenbosch University, within 150 km of all sites, where conditions were kept as close to natural as possible. The samples were air-dried, and then passed through a 1-mm mesh sieve to allow for even spread of the soil in labelled trays. The fine leaf litter contents that remained after sieving were incorporated into the sample trays as it was suspected that many of the smaller seeds were contained in the mass. All of the larger seeds that were noted were also incorporated into the sample. However seed counting was not done as seeds were hidden in the leaf litter and because seed germinability relates more strongly to restoration potential than seed density. Smoke treatment was equally distributed throughout all trays on the same day (11 May 2005, 1 May 2006) by means of a diluted liquid chemical concentrate (Kirstenbosch's Seed Primer Plus Liquid Concentrate Solution at a ratio of 1 part concentrate for every 9 parts water, totalling 20 l of diluted smoke treatment). Previous research has shown that many fynbos species use the chemicals found in the smoke water as a germination cue (Brown and Van Staden, 1997) and it is suspected that many riparian species respond positively to such germination cues. Some riparian species require seed abrasion to initiate germination (Leck, 1989; Fenner and Thompson, 2005), and this process was allowed for through the abrasive sieving process. The trays were then left for 24 h to absorb the treatment before irrigation commenced. Trays were kept moist with a fine spray irrigation system set on an automatic cycle with regular adjustments according to outdoor variations in moisture and temperature. The maximum and minimum temperatures recorded during the study period were 38 °C and 8 °C (2005), and 39 °C and 5 °C (2006), respectively.

Seedlings that emerged from the soil seed bank were counted and identified as close to species level as possible. Monitoring took place twice a month for the first three months, and monthly for the last three months. Abundance of seedlings per plot was converted into a scale based on the seedling counts/m^2 in order to get a classification of the seed bank groupings through the TWINSPAN analysis programme. Index values were assigned as follows: 0 seedlings/m^2: index = 0; 1–19: 1; 20–39: 2; 40–59: 3; 60–79: 4; >80: 5. The ecological information recorded for each quadrat, including species presence and percentage canopy cover, % rock cover and % bare ground, together with an estimate of total canopy cover for the quadrat, was used in the aboveground vegetation/seed bank species comparisons.

2.2. Data analysis

2.2.1. Vegetation and seed bank comparisons

Aboveground vegetation in each quadrat (1 m^2) was compared with the relevant seed bank sample collected. The experimental unit for all analyses is the plot (i.e. all quadrat samples were pooled together per plot and comparisons were done at plot level) and results are reported as species per m^2. The programme *Species Diversity and Richness* (Seaby and Henderson, 2005) was used to calculate Sørensen's Community Coefficient (Ss) on the combined data set (all species, alien and indigenous) between vegetation and seed bank communities: $Ss = 2C/(A+B)$, where C is the number of species common to both samples, and A and B are the number of species in sample A and B respectively (Kent and Coker, 1992). In this study A refers to the species that germinated from the seed bank samples, and B refers to the aboveground vegetation sampled. Comparisons were made of the degree of similarity between reference and invaded plots, as well

Table 1
Total species richness (in the seed bank) and seedling abundance for reference and invaded stream segments of four rivers sampled in the Western Cape, South Africa (Berg, Eerste, Molenaars and Wit)

River	Section	Seed bank Richness (per m^2)	Seedling Abundance (per m^2)
BERG	MS Ref	18.0	10.01
	MS Inv	11.4	2.31
	FH Ref	17.3	19.50
	FH Inv	10.0	3.19
EERSTE	MS Ref	15.3	8.13
	MS Inv	12.3	4.90
	FH Ref	21.0	10.43
	FH Inv	12.3	6.32
MOLENAARS	MS Ref	15.6	10.22
	MS Inv	23.0	5.56
	FH Ref	13.3	7.45
	FH Inv	17.0	5.75
WIT	MS Ref	12.3	7.08
	MS Inv	22.0	8.05
	FH Ref	10.5	4.47
	FH Inv	17.5	5.55

Only the indigenous species of the seed bank data were analysed (see text). MS = mountain stream, FH = foothill, Ref = reference, Inv = invaded. Seed bank sampling intensity was 10% of total plot. Total area sampled for the seed bank was 3 m^2 for all sections.

as between above- and below-ground species assemblages. To investigate the level of overlap, tables were compiled of the 20 most frequently occurring species (the most abundant and most common across plots) in invaded vs. un-invaded samples. Finally, Simpson's Index of diversity was to measure diversity levels in different sections of the rivers as it weights the most abundant species more heavily than the rare species. The formula measures the probability that two individuals randomly selected from a sample will be of different species. If n_i is the number of individuals i of species s which are counted, and N is the total number of all individuals counted, then the following formula is an estimator for Simpson's index (D) without replacement:

$$D = \sum_{i=1}^{s} \frac{n_i(n_i - 1)}{N(N - 1)}.$$

The 1-D value was expressed as the index as it then reflects highest diversity with highest value (Kent and Coker, 1992).

2.2.2. Seed bank community classification

The combined data set for seed banks (reference and invaded) was entered into the TurboVeg (Hennekens, 1996) programme. Community classification was conducted on the data using TWINSPAN (Two-way Indicator Species Analysis) (Hill, 1979) in Megatab (Hennekens, 1996). This raw data table was then repeatedly rearranged to group species with similar associations until a differentiated table was produced. Diagnostic species distinguish between communities by their presence in some communities and their absence in others (Whittaker, 1975). This classification was stopped at the second level of division to avoid generating meaningless communities. Results were interpreted in terms of communities and subcommunities. This approach was used to highlight patterns within seed banks of the sampled habitats and allowed us to compare community composition between reference and invaded sites.

2.2.3. Correspondence analysis

Using correspondence analysis in the programme *Statistica* 7.0 (StatSoft Inc., 2004), the twenty most frequently occurring, and thus influential, species from the reference and invaded seed bank data set were analysed independently. The results were interpreted in terms of the species assemblages that were evident before and after invasion. Not all species were included in the analysis because many species were rare and are of less interest for restoration efforts, given that the primary aim of restoration is to restore function which is driven by dominant species.

3. Results

3.1. Vegetation and seed bank comparisons

Our analyses are not hypothesis-driven but rather describe patterns and provide indications of important trends. Overall, the seed bank communities were richer in species than the above-ground vegetation communities, regardless of state (reference or invaded; data not shown). The general trend was that abundance of species in the seed bank decreased after invasion (Table 1), specifically for shrubs/shrublets and herbaceous perennials (Table 2). There was generally a low correspondence of species between aboveground and seed bank communities (Table 3). Sørensen's Community Coefficient for comparisons between aboveground vegetation and seed bank communities showed that within the foothill sections of both the Berg and Molenaars Rivers, as well as the mountain stream section of the Eerste and Molenaars Rivers, the similarity increased after invasion (Table 4). In only 3 out of 8 cases did the similarity index

Table 2
Seed bank seedling abundance (number per m^2) for reference and invaded sections of four rivers (Berg, Eerste, Molenaars and Wit) sampled

State RIVER	Ref BERG	Inv BERG	Ref EERSTE	Inv EERSTE	Ref MOL	Inv MOL	Ref WIT	Inv WIT
Tree	0	0	0.04	0	0	0	0	0
Shrub/shrublet	1.12	0.04	0.50	0.16	0.58	0.66	0.79	0.40
Herbaceous perennial	2.56	0.25	1.23	0.91	2.07	0.60	0.13	0.76
Succulent	10.36	0.03	0.10	0.59	0.19	0.14	0.13	0.43
Herbaceous annual	1.80	0.69	1.35	1.32	0.73	1.00	0.30	1.77
Graminoid	8.91	1.74	4.36	2.62	5.26	3.27	3.26	2.08

Data are divided into growth forms. Only the indigenous species of the seed bank data were analysed (see text).

Table 3
The 20 most frequently occurring species in riparian aboveground vegetation and soil seed banks (seedling emergents) samples taken from reference and invaded sections along four rivers in the Western Cape, South Africa (Berg, Eerste, Molenaars & Wit Rivers)

Reference						Invaded					
Aboveground vegetation			Seed bank seedlings			Aboveground vegetation			Seed bank seedlings		
Family	Botanical name	Freq. (%)	Family	Botanical name	Freq. (%)	Family	Botanical name	Freq. (%)	Family	Botanical name	Freq. (%)
ASTERACEAE	*Brachylaena neriifolia*	76	POACEAE	*Pennisetum macrourum*	100	FABACEAE	**Acacia mearnsii*	100	OXALIDACEAE	**Oxalis corniculata*	100
MYRTACEAE	*Metrosideros angustifolia*	72	POACEAE	*Pentaschistus pallida*	100	MYRTACEAE	*Metrosideros angustifolia*	40	EUPHORBIACEAE	**Euphorbia prostrata*	96
PROTEACEAE	*Brabejum stellatifolium*	64	JUNCACEAE	*Juncus capensis*	98	COMMELINACEAE	*Commelina benghalensis*	36	ASTERACEAE	**Conyza albida*	91
RESTIONACEAE	*Calopsis paniculata*	52	CYPERACEAE	*Ficinia anceps*	96	MYRTACEAE	**Eucalyptus camaldulensis*	32	BRASSICACEAE	**Nasturtium officinale*	91
ERICACEAE	*Erica caffra* var caffra	48	RESTIONACEAE	*Ischryrolepis subverticillata*	91	POACEAE	*Erharta longiflora*	24	CYPERACEAE	*Isolepis prolifera*	83
POACEAE	*Pennisetum macrourum*	44	POACEAE	*Panicum schinzii*	87	ASTERACEAE	*Brachylaena neriifolia*	24	POACEAE	*Pentaschistis pallida*	83
BLECHNACEAE	*Blechnum capense*	40	ASTERACEAE	*Pseudognaphalium luteo-album*	82	DRYOPTERIDACEAE	*Prionium serratum*	16	CYPERACEAE	*Ficina anceps*	79
RESTIONACEAE	*Ischyrolepis subverticillata*	28	ASTERACEAE	*Senecio cordifolius*	78	FABACEAE	**Sesbania punicea*	16	VERBENACEAE	**Verbena bonariensis*	79
PRIONIACEAE	*Prionium serraturm*	28	CYPERACEAE	*Isolepis prolifera*	78	ANACARDIACEAE	*Rhus angustifolia*	16	FABACEAE	**Acacia mearnsii*	79
RESTIONACEAE	*Elegia capensis*	28	ASTERACEAE	*Helichrysum helianthemifolium*	74	POACEAE	*Cynodon dactylon*	12	ERICACEAE	*Erica* sp. 1	71
FABACEAE	**Acacia mearnsii*	28	THYMELACEAE	*Struthiola tomentosa*	74	BLECHNACEAE	*Blechnum capense*	12	JUNCACEAE	*Juncus capensis*	66
JUNCACEAE	*Juncus capensis*	24	ASTERACEAE	*Euryops abrotanifolius*	74	AQUIFOLIACEAE	*Ilex mitis*. var. mitis	12	ASTERACEAE	*Metalasia* sp. 1	66
ASTERACEAE	*Metalasia* sp. 1	24	ERICACEAE	*Erica* sp. 1	70	PROTEACEAE	*Brabejum stellatifolium*	5	CAMPANULACEAE	*Wahlenbergia obovata*	63
MYRICACEAE	*Morella serrata*	24	CAMPANULACEAE	*Wahlenbergia cernua*	70	FABACEAE	**Acacia longifolia*	4	POACEAE	*Digitaria debilis*	63
AQUIFOLIACEAE	*Ilex mitis* var. mitis	24	SOLANACEAE	**Solanum nigrum*	65	RESTIONACEAE	*Elegia capensis*	2	CRASSULACEAE	*Crassula* sp. 1	58
RESTIONACEAE	*Cannomois virgata*	20	ASTERACEAE	**Hypochaeris radicata*	61	CYPERACEAE	*Isolepis prolifera*	1	ASTERACEAE	**Phytolacca octandra*	54
ASTERACEAE	*Euryops abrotanifolius*	20	ROSACEAE	*Cliffortia cuneata*	61	AMARANTHACEAE	**Amaranthus deflexus*	1	POACEAE	*Ehrharta longiflora*	54
RESTIONACEAE	*Rhodocoma capensis*	20	MESEMBRYANTHEMACEAE	*Erepsia*/ *Carpobrotus* sp	39	PRIONIACEAE	*Prionium serratum*	1	ASTERACEAE	*Senecio polyanthemoides*	46
ERICACEAE	*Erica* sp. 1	20	SCROPHULARIACEAE	*Pseudoselago serrata*	39	SOLANACEAE	**Solanum mauritianum*	1	FABACEAE	**Melilotus indica*	42
ASTERACEAE	*Helichrysum* sp.	12	ASTERACEAE	*Metalasia* sp. 1	10	ERICACEAE	*Erica caffra* var caffra	1	GERANIACEAE	*Pelargonium iocastum*	29

$n=290$ samples (reference) and $n=310$ (invaded).
Data are presented in descending order of frequency. Nomenclature follows Germishuizen et al., 2006. * = Alien species. Freq. = Frequency of occurrence (in %).

decrease after invasion (Table 4). Comparison based on growth forms (Table 2) showed similar patterns of a community shift throughout most post-invaded plots, whereby the aboveground vegetation was predominantly alien invasive tree species, while the seed bank was composed of graminoids, herbaceous annuals and agricultural weedy species, with few species overlapping (summarised in Table 3). In contrast, comparisons between reference plots showed that community structure was more similar in terms of a stronger shrub/shrublet presence in both the aboveground and seed bank communities and several herbaceous perennials overlapped (Table 2 and summarised in Table 3). There were few shared species between aboveground vegetation and seed bank communities of invaded sections. These comprised mainly invasive woody species (**A. mearnsii*), and a few indigenous graminoids (*Ehrharta longiflora* and *Isolepis prolifera*) (Table 3). Alien species are marked with an asterisk. In contrast, the overlapping species within the reference samples were all indigenous species, mainly shrub/shrublets (*Erica* sp., *Euryops abrotanifolius*, *Ischyrolepis subverticillata*, and *Metalasia* sp. 1) and few herbaceous graminoid species (e.g. *Juncus capensis, Pennisetum macrourum*). The seed bank community in reference samples contained some alien annual species that were rare or not present in the aboveground vegetation. For example, **Solanum nigrum* was fairly abundant in the reference seed bank community but was noted as being present only once in the aboveground vegetation. A few species were in high abundance within both the reference and invaded seed bank samples (*Ficinia anceps* and *J. capensis*). Those species abundant in the invaded samples included **Euphorbia prostrata *Oxalis corniculata*, *I. prolifera* and **A. mearnsii*, while species abundant within the reference seed bank samples included *P. macrourum, Pentaschistus pallida, Ischryrolepis subverticillata* and *Pseudoganaphalium luteo-album*.

Table 4
Sørensen's Community Coefficient (Ss) for comparison between vegetation and seed banks in fynbos riparian plots sampled along four rivers in the Western Cape, South Africa

River/reach/state	Sørensen's index
BERG/MS/ref	0.28
BERG/MS/inv	0.21
EERSTE/MS/ref	0.14
EERSTE/MS/inv	0.41
MOLENAARS/MS/ref	0.11
MOLENAARS/MS/inv	0.22
WIT/MS/ref	0.28
WIT/MS/inv	0.28
BERG/FH/ref	0.31
BERG/FH/inv	0.38
EERSTE/FH/ref	0.56
EERSTE/FH/inv	0.25
MOLENAARS/FH/ref	0.13
MOLENAARS/FH/inv	0.15
WIT/FH/ref	0.53
WIT/FH/inv	0.10

Samples (invaded = 310 quadrats, reference = 290 quadrats) were pooled together and compared at plot level (see text).
Code for river system is River (Berg, Eerste. Molenaars, Wit)/reach (MS = mountain stream, FH = foothill)/state (ref = reference, inv = invaded).

3.2. Seed bank community classification

The floristic classification indicates that two main seed bank communities, A (invaded states of all rivers) and B (reference states of all rivers), are contained in this data set. A third, transitional community from a single site (Invaded Wit river mountain stream) was identified. Each main community consisted of several subcommunities (A1–A4; B1–B4), which were either typical subcommunities or "forms" of subcommunities. Most species in the seed bank were identified as pioneer species, while both fynbos and riparian elements were present. The results of the analysis are shown in the summary of Table 5 (and full table, available online as Appendix A) and are summarized below.

3.2.1. Euphorbia prostrata–Nasturtium officinale community (A)

Eleven of the differential species in this community are exotic which indicates that this is a highly modified community that is diagnostic of invaded sites. The indigenous species that were grouped within this community are those often associated with disturbed areas such as *Senecio polyanthemoides, Pelargonium elongatum*, and several graminoid species. The community is further divided into three subcommunities:

3.2.1.1. Typicum subcommunity (A4). This subcommunity group occurred across all 4 rivers, within both the mountain stream and foothill sections and was dominated by a cocktail of exotic and invasive species and indigenous weeds.

3.2.1.2. Euphorbia prostrata–Pelargonium iocastum subcommunity. The differential species in this subcommunity are the exotic perennial herb, *E. prostrata* and the dwarf shrub *Struthiola striata*. There are two forms within this subcommunity:

- *Arctotheca calendula* form (A1): Situated in the invaded mountain stream sections of the Wit and Eerste rivers, dominant species are the herbs, *A. calendula* and *Apium inundatum*.
- *Leptospermum laevigatum* form (A2): Situated in the foothill sections of the Eerste and a mountain stream section of the Berg and Molenaars, this form is dominated by the perennial tree/shrub, *L. laevigatum*.

3.2.1.3. Euphorbia prostrata–Paraserianthes lophantha subcommunity (A3). This subcommunity is dominated by the invasive tree, *P. lophantha*, and is found in the invaded foothill and mountain stream sections of the Molenaars and Berg rivers and a single invaded foothill site on the Eerste river.

3.2.2. Pennisetum macrourum–Anthospermum sp. 1 community (B)

This community (Group B) is diagnostic to the reference sites (of all rivers) and was dominated by graminoids, herbaceous perennials and longer-lived woody shrubs. The few alien species that were present were annuals that are usually associated with agricultural and disturbed landscapes (e.g. **Aira cupaniana*, **Hypochaeris radicata*, **Lactuca serriola*, **Anagallis arvensis* subsp. *arvensis*). Of the species present in this community, *P. macrourum*, *Anthosperumum* sp. 1, *Struthiola*

Table 5
Summary table of seed bank communities among four rivers (Berg, Eerste, Molenaars and Wit) sampled in the Western Cape, South Africa. Data of species fidelity (%) to each community (A1–A4, B1–B4 and Tr, transitional) are summarized from the Appendix A, available online

	Summary table of species fidelity (%) to community									Number of	
										Plots	Communities
	A1	A2	A3	A4	B1	B2	B3	B4	Tr	62	9
Differential species of the Euphorbia prostrata–Nasturtium officinale community											
* *Euphorbia prostrata*	100	100	89	100					100	30	5
* *Nasturtium officinale*	100	100	89	82					100	28	5
* *Conyza albida*	100	100	100	64					100	27	5
* *Acacia mearnsii*	100	67	89	82					100	26	5
* *Briza maxima/Briza minor*	50	83	67	73						21	4
* *Phytolacca octandra*	25	83	67	73			11			21	5
Ehrharta longiflora	75	67	67	64						20	4
Senecio polyanthemoides	50	83	100	18		11				19	5
Pentaschistus pallida	75	67	33	55						16	4
Crassula sp. 1	100	33	56	18					100	14	5
* *Rubus* sp.	100	50	33	18			11			13	5
Prismatocarpus fruticosus	75	33	44	27						12	4
* *Sonchus asper*	75	50	22	18			11			11	5
* *Melilotus indica*	75	50	22	9					100	10	5
Pelargonium elongatum	75	17	33	9						8	4
Nemesia versicolor	25	17	56	18						9	4
* *Sesbania punicea*	25		33	27					100	8	4
Cynodon dactylon	25	33	22	18					100	8	5
* *Geranium molle*	25	17	11							3	3
Crassula sp. 1	50		11							3	2
Hibiscus trionum	50		11							3	2
Mesemb. sp. 1		17	11	9						3	3
Differential species of the Arctotheca calendula form of the Euphorbia prostrate–Pelargonium iocastum subcommunity											
Arcotheca calendula	100									4	1
Apium inundatum	100									4	1
* *Fumaria muralis* subsp. *muralis*	75									3	1
Dorotheanthus bellidiformis subsp. *bellidiformis*	75			9						4	2
Differential species of the Leptospermum laevigatum form of the Euphorbia prostrata–Pelargonium iocastum subcommunity											
* *Leptospermum laevigatum*		83				11				6	2
Commelina benghalensis		67		9						5	2
Oxalis pes-caprae		50								3	1
Differential species of the Euphorbia prostrata–Pelargonium iocastum subcommunity											
Pelargonium iocastum	100	50								7	2
Struthiola striata	25	17								2	2
Differential species of the *Euphorbia prostrata–Paraserianthes lophantha* subcommunity											
* *Paraserianthes lophantha*		33	44							6	2
* *Amaranthus deflexus*		50	33							6	2
Crassula natans var. natans		50	33	0						6	3
Setaria verticillata		17	22							3	2
Pentaschistus curvifolia		17	22	9						4	3
* *Poa annua*		17	11							2	2
Scroph sp 1			44							4	1
Erica sp. 1			22							2	1
Differential species of the Pennisetum macrourum–Anthospermum sp. 1 community											
Pennisetum macrourum					100	89	78	67		25	4
Anthospermum sp.					75	56	67	33		17	4
Senecio sp.					100	56	67	22		17	4
Pseudoselago quadrangularis					100	44	56	22		15	4
Crassula thunbergiana					50	67	33	33		14	4
Crassula pellucida subsp *pellucida*					50	22	11	22		7	4
* *Aira cupaniana*					25	22	11	22		6	4

Table 5 (*continued*)

	Summary table of species fidelity (%) to community									Number of	
										Plots	Communities
	A1	A2	A3	A4	B1	B2	B3	B4	Tr	62	9
Differential species of the Erica caffra form of the Pennisetum macrourum–Struthiola tomentosa subcommunity											
Erica caffra					50				100	3	2
Roella sp.					75				100	4	2
Siphocodon debilis					50					2	1
Differential species of the Agathosma crenulata form of the Pennisetum macrourum–Struthiola tomentosa subcommunity											
Agathosma crenulata						78				7	1
Ilex mitis						33				3	1
Cliffortia strobilifera						22				2	1
Species common to communities B1 and B2											
Cliffortia grandifolia					25	56				6	2
Zaluzianskya capensis					25	44				5	2
Rhynchosia capensis					25	33				4	2
Cunonia capensis					25	11				2	2
Differential species of the Pennisetum macrourum–Struthiola tomentosa subcommunity											
Struthiola tomentosa				18	75	78	89		100	21	5
Argyrolobium lunare					75		56			8	2
Crassula coccinea					75	22	44			9	3
Disparago sp.					50	33	22			7	3
Cotula australis					25	44	22			7	3
Monopsis lutea					25	22	11			4	3
Empleurum unicapsulare					25		11			2	2
Species common to Community A and subcommunities B1–B3											
Wahlenbergia obovata	100	67	78	55	25	11	11		100	25	8
Juncus sp.	75	33	44	27	50	33	22		100	20	8
Dischisma ciliatum	50	50	44	27	25	11	11			15	7
Oftia africana	25		33	36	25	11			100	11	6
Podalyria calyptrata	25	33	0	9	50	22	22			10	7
* *Acacia longifolia*		33	33	36		33	22			14	5
Roella sp.			33	27	25	11	11			9	5
* *Lactuca serriola*	50		0	9	75	44	22			12	6
Crassula tetragona	25		22	27	25	11				8	5
Berzelia lanuginosa		33	11	18	50	22			100	10	6
Chironia sp.	25		0		75	11	22			7	5
Seriphium plumosa	25		22		75	33				9	4
Ursinia paleaceae			11	9		22	22			6	4
Centella sp.			11			22	56			8	3
Pelargonium cucullatum	25		0			22	11			4	4
Struthiola myrsinites/S. striata		17	0	18			11			4	4
Widespread species found throughout the study area											
Schoenoplectus sp.	50	100	100	91	100	100	100	78	100	57	9
Metalasia sp.	100	100	89	55	100	100	100	100	100	56	9
Juncus capensis	25	83	89	82	100	100	100	89	100	54	9
Ficinia anceps	100	100	100	73	75	78	100	67	100	53	9
Isolepis prolifera	75	100	100	73	100	100	56	44	100	49	9
Pseudognaphalium luteo-album	100	83	56	73	100	89	56	67	100	46	9
Helichrysum helianthemifolium	100	50	89	45	100	78	56	56	100	42	9
Ischyrolepis subverticillata	25	50	56	45	100	89	89	78		41	8
* *Oxalis corniculata*	100	100	100	100	75	22	22	11	100	39	9
Panicum schinzii	25	100	78	36	75	78	67	33	100	38	9
Senecio cordifolius	25	17	78	18	100	100	67	44	100	35	9
Solanum retroflexum	100	50	44	27	100	44	78	44	100	34	9
* *Verbena bonariensis*	100	100	89	55	50	22	22	22	100	33	9
Digitaria debilis		67	44	55	50	67	44	33	100	30	8
Euryops abrotanifolius		17	56		100	67	89	22	100	27	7
Wahlenbergia cernua	75	17	11		100	89	78	33		27	7
* *Hypochaeris radicata*	75	50	11		50	78	78	33		26	7

(continued on next page)

Table 5 (*continued*)

	Summary table of species fidelity (%) to community									Number of	
										Plots	Communities
	A1	A2	A3	A4	B1	B2	B3	B4	Tr	62	9
* *Spergula arvensis*	25	17	22	27	75	22	78	44		23	8
Psoraleae sp.	25				50	78	78	56		22	5
* *Anagallis arvensis*	50				100	56	67	33		20	5
Scirpus sp.	25		11		75	56	67	33		19	6
Cliffortia ruscifolia	25		44	18	50	33	44	11		17	7
* *Polycarpon tetraphyllum*	50	67	33	27	50			22		16	6
Cliffortia cuneata				9	50	56	56	22		15	5
Pseudoselago serrata			11		75	67	33	22		15	5
* *Persicaria lapathifolia*		33	33	18	25	22	22	11	100	14	8
Othonna quinquedentata	25		33		100	33	22	11		14	6
Agrostis lachnantha		17	22		50	44	44	11		14	6
Pentameris sp.			11		75	44	44	11	100	14	6
Chrysanthemoides monilifera	25		22		50	22	44	22		13	6
Plantago lanceolata	25	33			75	44	22	11		13	6
Erepsia anceps			11		50	44	33	22		12	5
Carpobrotus sp.	25		11		50	11	11	11	100	8	7

Species occurring in a single plot: name, abundance value (plot number).
* *Acacia melanoxylon* 1 (57), *Drosera hiliaris* 1 (32), *Grubbia tomentosa* 1 (32), *Morella serrata* 1 (44), *Pelargonium papilionaceum* 1 (22), *Pelargonium* sp. 1 (22), *Polyarrhena reflexa* 1 (22), *Restio* sp. 1 (45), *Senecio* sp. 1 (4), * *Vicia benghalensis* 1.

tomentosa, *Senecio* sp. 1, and *Pseudoselago quadrangularis* occurred in high frequencies. The community is further divided into two subcommunities:

3.2.2.1. Typicum subcommunity (B4). This subcommunity group occurred across 3 of the 4 rivers (Berg, Molenaars and Wit), within both the mountain stream and foothill sections. The differential species are *P. macrourum*, a perennial grass; *Anthospermum* sp. a perennial shrub and two succulent *Crassula* spp.

3.2.2.2. Pennisetum macrourum–S. tomentosa subcommunity (B3). The differential species in this subcommunity are comprised of a mixture of dwarf shrubs, annual and perennial herbs with a single perennial tree/shrub, *Empleurum unicapsulare*. There are two forms within this subcommunity:

- *Erica caffra* form (B1): Situated in reference foothill and mountain stream sites on the Berg river, a reference foothill site on the Eerste and a reference mountain stream site on the Molenaars, differential species are *E. caffra*, an erect shrub or small tree and two perennial dwarf shrubs.
- *Agathosma crenulata* form (B2): Situated in reference foothill and mountain stream sites on the Eerste and Berg rivers and a reference mountain stream site on the Molenaars, differential species are the perennial shrub, *Agathosma crenulata* (buchu); perennial tree, *Ilex mitis* and perennial dwarf shrub, *Siphocodon debilis*.

3.3. Correspondence analysis

The correspondence analysis (Fig. 1) grouped species in the seed bank according to moisture regime of the habitat type. Within the reference samples, (Fig. 1A; Tables 5 and 6) association patterns of vegetation types and habitat moisture gradients were more clear with riparian species best represented within the wet bank zones and fynbos species similarly so within the dry bank zone. However, this pattern was not evident within the invaded samples (Fig. 1B; Tables 5 and 6). There was some overlap between species that occurred in both reference (A) and invaded (B) samples, and some of these species shifted in their association to particular habitat types after invasion (Tables 5 and 6).

4. Discussion

There was a clear impact of invasion on the composition and structure of riparian seed banks in this study. However, invaded riparian seed banks had sufficient diversity to initiate community recovery at the sites we studied.

4.1. To what extent do riparian seed banks have potential to regenerate vegetation that is structurally and compositionally similar to undisturbed riparian vegetation?

There was little overlap between species represented in soil seed banks and those present in the aboveground vegetation, as found in other studies (Leck, 1989; Thompson, 1992; Richter and Stromberg, 2005). Although the seed bank in reference sections of the sampled area showed a high diversity of indigenous species in most cases, there was a bias towards herbaceous growth forms; only a few common woody riparian species were represented in the seed bank. Considering the fluctuating dynamics, particularly within frequently disturbed habitats (such as fynbos riparian habitats), virtually all species that had viable seeds within the soil should have shown signs of germination within the trial time of six months. This study is the first to document the composition of seed banks of fynbos riparian areas, and it is clear that not all of the characteristic species of these areas are represented in the seed bank. It is suggested that introduction of species to provide a variety of

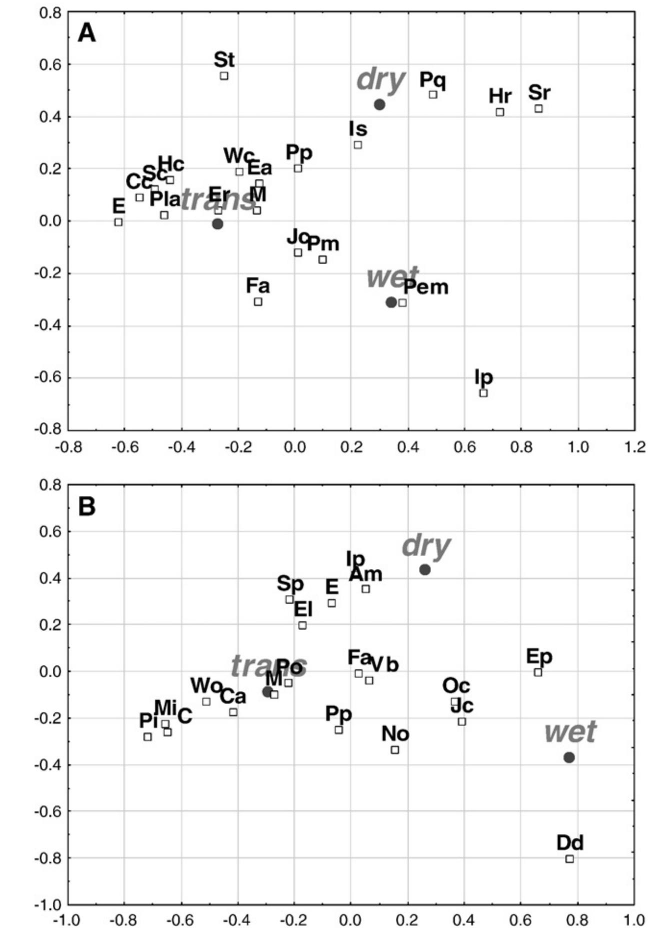

Fig. 1. Correspondence analysis of the 20 most frequent species in the seed bank at habitat scale. Samples were taken from reference (A) and invaded (B) sections of four rivers in the south-western part of the Western Cape, South Africa (see text). Trans = transitional bank zone. A: reference soil samples (Eigenvalue 1: 0.08854; Eigenvalue 2: 0.06451); B: invaded soil samples (Eigenvalue 1: 0.15769; Eigenvalue 2: 0.07022). Species codes: Am = **Acacia mearnsii*, C = *Crassula* sp., Ca = **Conyza albida*, Cc = *Cliffortia cuneata*, Dd = *Digitaria debilis*, E = *Erica* sp., Ea = *Euryops abrotanifolius*, El = *Erharta longiflora*, Ep = **Euphorbia prostrate*, Er = *Erepsia* sp., Fc = *Ficinia anceps*, Hh = *Helichrysum helianthemifolium*, Hr = **Hypochaeris radicata*, Ip = *Isolepis prolifera*, Is = *Ischyrolepis subvericillata*, Jc = *Juncus capensis*, M = *Metalasia* sp., Mi = **Melilotus indica*, No = **Nasturtium officinale*, Oc = **Oxalis corniculata*, Pem = *Pennisetum macrourum*, Pla = *Pseudognaphalium luteo-album*, Pm = *Panicum maximum*, Pi = *Pelargonium iocastum*, Po = *Phytolacca octandra*, Pp = *Pentaschistus pallida*, Pq = *Pseudoselago quadrangularis*, Sc = *Senecio cordifolius*, Sn = **Solanum nigrum*, Sp = *Senecio polyanthemoides*, St = *Struthiola tomentosa*, Vb = **Verbena bonariensis*, Wc = *Wahlenburgia cernua*, Wo = *Wahlenburgia obovata*. * = *Alien plant species* (see Appendix A, available online for full nomenclature).

structural growth forms (particularly tree and shrub species) must be considered if complete community integrity is intended to be restored (see Section 4.2).

Nilsson et al. (1989, 1991) examined entire rivers in northern Sweden and found that riparian vegetation was richest in species in the middle reaches of free-flowing rivers. Décamps and Tabacchi (1994) found similar patterns in French rivers. Our study shows slightly different results based on the seed bank data (above-mentioned studies were done exclusively on aboveground vegetation samples), where a fairly consistent pattern of higher species diversity in mountain stream sites compared to foothill sites was found (Appendix B available online; Fig. B1–4). This result was generally echoed in the aboveground vegetation survey data of this study (Vosse, 2006). The mountain stream sites generally experience lower levels of anthropogenic disturbance. In contrast, the foothill sites generally have a longer history of anthropogenic disturbance and may receive levels of disturbance that are too high to maintain community diversity. Consequently, the aboveground community becomes less diverse (although often still species-rich) and more homogenous, with pioneer species (such as *Psoralea* and *Helichrysum* species) and weedy agricultural species (**S. nigrum*, **Conyza albida*, **H. radicata*) dominating, as was found in this study. Additionally, the aboveground vegetation of the foothill slopes in this study was largely dominated by graminoids and herbaceous perennials from both fynbos and riparian vegetation types. In contrast, the extant vegetation found along mountain stream slopes studied tended to be dominated by long-lived woody fynbos shrubs, with some Southern Afrotemperate Forest elements well represented and more riparian species present and fewer fynbos species. Therefore, foothill sections of riparian areas may need assisted restoration techniques in order to restore community integrity more than mountain-stream sections.

Overall, we suggest that restoration efforts should be informed by the community composition in whatever areas remain intact. Further, assessments must be specific to each riparian zone, and should include consideration of past and future utilization requirements of the area. A recent study in a terrestrial landscape in the Mediterranean Basin by Buisson et al. (2006) found that site-specific variables contributed to 23% of the variation when

Table 6
The 20 most frequently occurring species in seed banks in reference and invaded samples taken from four rivers (Berg, Eerste, Molenaars and Wit) in the south-western part of the Western Cape, South Africa according to results from correspondence analysis (Fig. 1)

Reference	Habitat	Invaded
Isolepis prolifera	Wet bank zone	*Digitaria debilis*
Pennisetum macrourum		* *Nasturtium officinale*
Ficinia anceps		* *Oxalis corniculata*
Juncus capensis		***Juncus capensis***
Panicum maximum		**Euphorbia prostrata*
Wahlenbergia cernua		***Panicum schinzii***
***Metalasia* sp.**	Transitional bank zone	* *Verbena bonariensis*
Erepsia sp. 1		*Crassula* sp. 1
Euryops abrotanifolius		***Metalasia* sp. 1**
Panicum schinzii		* *Phytolacca octandra*
Pseudognaphalium luteo-album		* *Conyza albida*
***Erica* sp. 1**		*Wahlenbergia obovata*
Cliffortia cuneata		***Ficinia anceps***
Senecio cordifolius	Dry bank zone	*Pelargonium iocastum*
Helichrysum helianthemifolium		* *Melilotus indica*
Struthiola tomentosa		* *Acacia mearnsii*
Ischryrolepis subverticillata		***Isolepis prolifera***
Pseudoselago quadrangularis		*Senecio polyanthemoides*
**Hypochaeris radicata*		*Erharta longiflora*
**Solanum nigrum*		***Erica* sp. 1**

Overlapping species are indicated in bold. Nomenclature follows Germishuizen et al. (2006). * = Alien plant species.

investigating the seed bank patterns in relation to plant succession at the edges of abandoned fields. They found each site to be characterised by a unique history which had a direct influence on the particular set of species found. Such variation in historical land-use, together with the extreme variability of both riparian areas and seed banks, makes evaluating the restoration potential of riparian seed banks on a broad scale very difficult.

4.2. What happens to the species composition of the seed bank after invasion and is it adequate to initiate ecosystem recovery?

We found a clear pattern of decline in community integrity after invasion, both in terms of species richness and density (Table 1). Species richness tended to show similar patterns of decline, although not through all samples. The entire Wit (mountain stream and foothill) and foothill section of the Molenaars rivers showed an increase in species richness; this was thought to be related to site history. Both rivers have had a long history of anthropogenic disturbance from agricultural water abstraction and invasive alien plants. The community structure within the invaded sections of these rivers may be altered to such a degree that a unique, emergent community type may be forming. Additionally, the analyses at habitat scale showed some overlapping species shifting between habitat type after invasion (Fig. 1; Table 6). This was to be expected as trends within terrestrial landscapes show a more homogenous community persisting after invasion, particularly after long-term invasion (Holmes, 2002). Such a shift will have implications for restoration techniques needed to restore community integrity and will most probably require re-introductions of species lacking in the seed bank community following invasive alien-plant clearing.

Overall, this study found that even after heavy invasion, the seed bank was diverse enough to initiate community restoration. Seed banks were often dominated by indigenous herbaceous/ graminoid species, but some key riparian species were absent. These sites therefore require re-introduction of species to complete the restoration process. The value of maintaining a seed source for the woody, animal-dispersed riparian species cannot be overlooked (Wassie and Teketay, 2006). It is suggested that in areas where such seed sources are lacking, re-introductions in the form of planting propagated specimens should be part of the post-disturbance restoration process. Without this vital step, restoration is likely to be unsuccessful, and may result in the re-establishment of IAPs.

4.3. What are the implications for riparian restoration in the Western Cape?

In most cases, restoration of alien-invaded riparian vegetation in South Africa is fairly crude and aims simply to return key elements of ecosystem functioning. This study has shown that there is potential for self repair to be initiated, even in sites that have been heavily invaded. Not all elements regularly return unaided. Herbaceous and low-shrub growth forms generally dominate the seed bank, implying that these elements of the community are able to persist under invasion and can actively return to the restored system without the need for re-introduction. However, certain common riparian species were absent from seed banks, including woody elements with high biomass and functional importance in these systems (e.g. *Brabejum stellatifolium*, *Metrosideros angustifolia*, *Morella serrata*). These species need to be re-introduced either through planting or through natural dispersal from intact sections in the upper catchment. The whole cleared area need not be replanted with these riparian scrub species, but seed sources need to be created from where these species that do not recruit from the seed bank can disperse across the site (Sedell and Reeves, 1990; Wassie and Teketay, 2006). More research is needed on the life-history strategies of prominent riparian scrub species. It is also important to gain a better understanding of other aspects of seed bank dynamics and recruitment such, as dispersal, seed longevity and germination cues within riparian communities. On a finer scale, our study shows that species in the seed bank tend to group within different moisture regimes, while Swift et al. (2008-this issue) provide a mechanistic understanding of spatial distributions in relation to drought tolerance. Such knowledge of species' ecological requirements, particularly of those species needing to be re-introduced, is highly valuable in restoration and can result in greater success rates. The level of success will in turn affect the financial implications for the overall restoration project. We suggest that close attention needs to be paid to environmental variation within sites and that, together with sound knowledge of key indigenous species propagation and growth requirements, restoration need not be a financial burden for either landowner or government programmes to undertake. Finally, the overall recovery of a cleared site is highly dependent on the quality and sensitivity of the alien clearing process, which allows for- or destroys indigenous seed bank initiation of community restoration.

Acknowledgements

Financial support through a core team member grant from the DST-NRF Centre for Invasion Biology (Karen Esler) and a grant from the Department of Water Affairs and Forestry, in collaboration with Working for Water (Targets for Ecosystem Repair in Riparian Ecosystems in Fynbos, Grassland and Savanna Biomes). Dr. Martin Kidd for commenting on an earlier draft and assisting with the statistical analysis of the data, and Shayne Fuller, Marina Faber and Phillipa Holme for help with field work, and Dr Charlie Boucher for assistance with the seed bank community classification. To the landowners of Bastiaanskloof Private Nature Reserve, Die Poort farm, Mont Rochelle Private Nature Reserve, Oaklands estate, Quin Rock wine estate, Rainbow End Farm, Tokara estate, and all the staff from WfW and CapeNature for allowing access to their land and assisting in finding sites.

Appendix A. Supplementary data

Full community table of seed bank communities among four rivers [Berg (Bg), Eerste (Er), Molenaars (Mol) and Wit (Wit)] sampled in the Western Cape, South Africa. Codes are: Habitat (w = Wet bank, d = dry bank, t = transitional zone); River/ reach (MS = mountain stream, FH = foothill); Invasion state (ref = reference, inv = invaded).

Appendix B. Supplementary data

Simpson's diversity index computed for all seed bank samples collected along four rivers (Berg, Eerste, Molenaars and Wit) in the Western Cape, South Africa. Codes are as follows: Ref=Reference; Inv=Invaded; Er=Eerste River; Mol=Molenaars River; Bg=Berg River; MS=Mountain stream; FH=Foothill.

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2008.01.170.

References

Boucher, C., Tlale, S., 1999. Riparian and instream vegetation study. Unpublished report prepared for Lesotho Highlands Development Authority. Lesotho Highlands Water Project. Metsi Consultants, Maseru. Report 648-14

Brown, N.A.C., Van Staden, J., 1997. Smoke as a germination cue: a review. Plant Growth Regulation 22, 115–124.

Buisson, E., Dutoit, T., Torre, F., 2006. The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. Agriculture, Ecosystems & Environment 115, 6–14.

Bunn, S.E., Davies, P.M., Kellaway, D.M., Prosser, I.P., 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. Freshwater Biology 39, 171–179.

Cohn, J.P., 2001. Resurrecting the dammed: a look at Colorado River restoration. Bioscience 51, 998–1003.

Davies, B.R., Day, J.A., 1998. Vanishing Waters. University of Cape Town Press, Rondebosch.

Décamps, H., Tabacchi, E., 1994. Species richness along river margins. In: Hildrew, A.G., Giller, P.S., Raffaelli, D. (Eds.), Aquatic Ecology: Scale, Pattern and Process. Blackwell Scientific Publications, Oxford, United Kingdom, pp. 1–20.

Fenner, M., Thompson, K., 2005. Soil seed banks. In: Fenner, M., Thompson, K. (Eds.), The Ecology of Seeds. Cambridge University Press, Cambridge, pp. 251–320.

Galatowitsch, S.M., Richardson, D.M., 2005. Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape. Biological Conservation 122, 509–521.

Germishuizen, G., Meyer, N.L., Steenkamp, Y., Keith, M. (Eds.), 2006. A Checklist of South African Plants. South African Botanical Diversity Network Report No 41. SABONET, Pretoria.

Goodson, J.M., Gurnell, A.M., Angold, P.G., Morrissey, I.P., 2001. Riparian seed banks: structure, process & implications for riparian management. Progress in Physical Geography 25, 301–325.

Harms, R.S., Hiebert, R.D., 2006. Vegetation response following invasive Tamarisk (*Tamarix* spp.) removal and implications for riparian restoration. Restoration Ecology 14, 461–472.

Hennekens, S.M., 1996. MEGATAB. A Visual Editor for Phytosociological Tables. Version 1.0, Griesen and Geurts, Ulft.

Hill, M.O., 1979. TWINSPAN — A Fortran Programme for Arranging Multivariate Data in An Ordered Two-Way Table by Classification of the Individuals and Attributes. Section of Ecology and Systematics, Cornell University, Ithaca New York.

Holmes, P.M., 1998. Fynbos biome. In: Van der Heyden (Ed.), Rehabilitation Following Clearing of Invasive Alien Vegetation in South African Ecosystems: A Preliminary Review of Best Management Practices. CSIR Report Draft ENV/S- C 98109.

Holmes, P.M., 2001. A comparison of the impact of winter versus summer burning of slash fuel in alien-invaded fynbos areas in the Western Cape. Southern African Forestry Journal 192, 41–49.

Holmes, P.M., 2002. Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. Austral Ecology 27, 110–120.

Holmes, P.M., Richardson, D.M., 1999. Protocols for restoration based on recruitment dynamics, community structure and ecosystem function: perspectives from South African fynbos. Restoration Ecology 7, 215–230.

Holmes, P.M., Marais, C., 2000. Impacts of alien plant control on vegetation in the mountain catchments of the Western Cape. Southern African Forestry Journal 189, 113–117.

Kent, M., Coker, P., 1992. Vegetation Description and Analysis: A Practical Approach. Belhaven Press, London.

Ladd, P.G., Crosti, R., Pignati, S., 2005. Vegetative and seedling regeneration after fire in planted Sardinian pinewood compared with that in other areas of Mediterranean-type climate. Journal of Biogeography 32, 85–98.

Leck, M.A., 1989. Wetland seed banks. In: Leck, M.A., Parker, T.V., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press Inc., San Diego, pp. 283–303.

Muotka, T., Laasonen, P., 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39, 145–156.

Musil, C.F., De Witt, D.M., 1990. Post-fire regeneration in a sand plain lowland fynbos community. South African Journal of Botany 56, 167–184.

Nilsson, C., Grelsson, G., Johansson, M., Sperens, U., 1989. Patterns of plant species richness along riverbanks. Ecology 70, 77–84.

Nilsson, C., Gardfjell, M., Grelsson, G., 1991. Importance of hydrochory in structuring plant communities along rivers. Canadian Journal of Botany 69, 2631–2633.

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, C., Decamps, H., 1996. Invasibility of species rich communities in riparian zones. Conservation Biology 10, 598–607.

Prins, N., Holmes, P.M., Richardson, D.M., 2004. A reference framework for the restoration of riparian vegetation in the Western Cape, South Africa, degraded by invasive Australian Acacias. South African Journal of Botany 70, 767–776.

Renöfält, B.M., Nilsson, C., Jansson, R., 2005. Spatial and temporal patterns of species richness in a riparian landscape. Journal of Biogeography 32, 2025–2037.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasion. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, United Kingdom, pp. 535–570.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P., Hobbs, R.J., 2007. Riparian vegetation — degradation, alien plant invasions and restoration prospects. Diversity and Distributions 13, 126–139.

Richter, R., Stromberg, J.C., 2005. Soil seed banks of two montane riparian areas, implications for restoration. Biodiversity and Conservation 14, 993–1016.

Rowntree, K.M., 1991. An assessment of the potential impact of alien invasive vegetation on the geomorphology of river channels in South Africa. South African Journal of Aquatic Science 17, 28–43.

Rutherford, I.D., Jerie, K., Marsh, N., 2000. A Rehabilitation Manual for Australian Streams, Volumes 1 & 2. Cooperative Research Center for Catchment Hydrology & Land and Water Resources Research and Development Corporation. Canberra, Australia.

Seaby, R.M., Henderson, P.A., 2005. Species Diversity and Richness, Version 2.65. Pisces Conservation Ltd., Lymington, England.

Sedell, J.R., Reeves, G.H., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14, 711–724.

Statsoft Inc., 2004. STATISTICA (Data Analysis Software System). Version 7. www.statsoft.com.

Swift, C., Jacobs, S., Esler, K.J., 2008. Drought induced xylem embolism in four riparian trees from the Western Cape Province: insights and implications for planning and evaluation of restoration. South African Journal of Botany 74, 508–516 (this issue). doi:10.1016/j.sajb.2008.01.169.

Thompson, K., 1992. The functional ecology of seed banks. In: Fenner, M. (Ed.), Seeds. The Ecology of Regeneration in Plant Communities. CAB International, Wallingford, pp. 231–258.

Thompson, K., 1993. Seed persistence in soil. In: Hendry, G.A.F., Grime, J.P. (Eds.), Methods in Comparative Plant Ecology. Chapman and Hall, London, pp. 199–202.

Van der Valk, A.G., 1981. Succession in wetlands, a gleasonian approach. Ecology 62, 688–696.

Van Wilgen, B.W., Le Maitre, D.C., Cowling, R.M., 1998. Ecosystem services, efficiency, sustainability, and equity, South Africa's working for water programme. Trends in Ecology and Evolution 13, 378.

Vosse, S., 2006. The restoration potential of fynbos riparian seed banks following alien clearing. MSc Thesis. Stellenbosch University.
Warr, S.J., Thompson, K., Kent, M., 1993. Seed banks as a neglected area of biogeographic research, a review of literature and sampling techniques. Progress in Physical Geography 17, 329–347.
Wassie, A., Teketay, D., 2006. Soil seed banks in church forests of northern Ethiopia: implications for the conservation of woody plants. Flora (Jena) 201, 32–43.
Welling, C.H., Pederson, R.L., Van der Valk, A.G., 1988. Recruitment from the seed bank and the development of emergent zonation during drawdown in a prairie wetland. Journal of Ecology 76, 483–496.
Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan Publishing Company, New York.

Edited by ETF Witkowski